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THE APPARENT WATER-PERMEABILITY OF *CARCINUS MAENAS* (CRUSTACEA, BRACHYURA, PORTUNIDAE) AS A FUNCTION OF SALINITY

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There is general evidence (Potts and Parry, 1964, pp. 138–143) that the integumental water-permeability of crustaceans inhabiting fresh and brackish water is less than that of marine species, and the adaptive significance of this in reducing the osmotic work-load is obvious. But whether it is possible for an individual crustacean to alter its own water-permeability as an adaptive physiological response to an environmental change of salinity is not self-evident, and conflicting views have been published. Rudy (1967), using tritiated water (T_2O) found adaptive differences in water-permeability among several different species of marine, brackish-water, and freshwater crustaceans, but stated on the basis of his data that the brackish-water, euryhaline, species *Palaemonetes varians* and *Carcinus maenas* could not significantly alter their integumental water permeability. However, I was able to demonstrate on the basis of the uptake of D_2O a significant reduction of water-permeability in response to lowered salinity in the very euryhaline crab *Rhithropanopeus harrisi* (Smith, 1967), and expressed the opinion that Rudy's data on *Carcinus* did not rule out such a response in the latter crab, although Rudy was correct in that his data did not show a statistically significant reduction of permeability. Because *Carcinus* is such an extensively studied animal, it seemed worthwhile to re-examine it by the same D_2O method used to demonstrate a water-permeability change in *Rhithropanopeus* and also in the polychaete worm *Nereis diversicolor* (Smith, 1970), to provide a basis for comparing *Carcinus* with less well known species in other waters.

Materials and Methods

Specimens of *Carcinus* of a wide range of sizes and of both sexes were collected in early June on the rocky marine shore near St. Mary's Island, Whitley Bay, Northumberland, in northeastern England. Soft or "paper-shelled" individuals were discarded, as were ovigerous females or crabs lacking one or more claws, or more than a couple of legs. Crabs were maintained at about 15° C at the Dove Marine Laboratory and were adapted for a week or longer in seawater (SW), and in 75%, 50%, 35% and 25% SW, in large plastic boxes provided with stones for shelter. Seawater in these experiments had a chloride concentration of 549 m*M*/l. Experiments were carried out at the Department of Zoology, University of Newcastle upon Tyne; the adapted crabs needed on a given day were brought to Newcastle in the morning and tested the same day at room temperature (18–19° C).

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Exposure to 5% D_2O in various dilutions of SW followed closely the method used by Smith (1967) for *Rhithropanopeus* except that exposure time was shortened to 15 minutes instead of 30, since *Carcinus* is considerably more permeable to D_2O than the former crab. Seawater was diluted by the addition of local Newcastle pondwater plus sufficient D_2O (90 moles %) to yield 75, 50, 35 and 25% SW. Since the addition of the D_2O to SW caused a dilution to 94% SW, crabs to be tested in this medium were placed in SW diluted to 94% SW with deionized water 2–3 hours before the tests. Crabs above 15 g in weight were tested in a liter of the 5% D_2O solutions, smaller crabs in 500 ml. At the end of each exposure the crab was removed, quickly dried in a cloth towel, and a few drops of blood drawn by puncture of the arthrodial membrane at a leg base. This

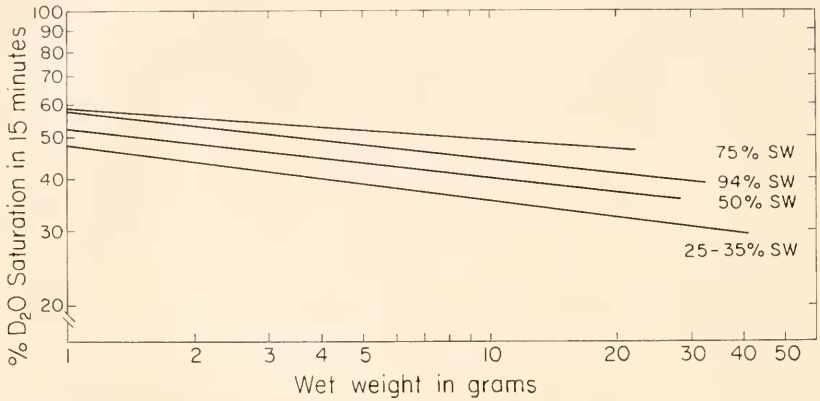

FIGURE 1. Curves relating D_2O-uptake (as % saturation attained in 15 min) to wet weight of *Carcinus* plotted by method of least squares. The equations—Uptake $= a(\text{weight})^{(b-1)}$—are: 94% SW, Uptake $= 57.85\ W^{(-0.1152)}$, $n = 23$; 75% SW, Uptake $= 58.45\ W^{(-0.0757)}$, $n = 11$; 50% SW, Uptake $= 52.07\ W^{(-0.1129)}$, $n = 12$; 25–35% SW, Uptake $= 48.37\ W^{(-0.1316)}$, $n = 22$.

sample was immediately placed in the large end of a Pasteur pipette, the pipette closed with a small cork, and its tip sealed in a flame. These pipettes, containing samples of blood and medium, were laid on a slide warmer overnight at 50° C to distill the water from the samples into the tips, which projected several inches from the warmer and were cooled by the evaporation of water from a strip of facial tissue paper laid across them with its ends dipping into beakers of water. D_2O contents of blood samples, controls, and the respective media were estimated by comparison with drops of standard solutions (0 to 5% D_2O) in a pair of kerosene/bromobenzene density gradient columns as in Smith's (1967) study of *Rhithropanopeus*. The method is described in detail in Welsh, Smith, and Kammer (1968, pp. 184–188). Values reported are the average of results from the two columns except in a few instances when one subsample was lost or when too little distillate was obtained for two determinations. In a given day's work, half the crabs used had been adapted to and were tested in a higher salinity, half in a lower. This permitted more effective use of the density gradients and helped to randomize differences in time of adaptation and room temperature.

Chloride determinations were made on separate samples from 50 of the 68 crabs tested, taken after the D_2O samples by means of disposable capillary pipettes (Drummond "microcaps"), discharged into 1 ml of deionized water before addition of the acid reagent used with the Aminco-Cotlove electrometric chloride titrator.

D_2O-uptake values were recorded as the per cent of the concentration of D_2O in the medium attained in the blood in 15 minutes, taking the D_2O content of the medium as 100%. Since D_2O uptake is weight-specific (Smith, 1967), these "% saturation" values (corrected for controls) were treated following the equation, $S = aW^{(b-1)}$ in which S = % saturation at 15 minutes, W = wet weight in grams, a = intercept on the ordinate at unit weight, and $(b-1)$ = slope in double log plot. The calculation of (a) and $(b-1)$ was by the method of least squares. For statistical treatment and the calculation of hourly water exchange fractions (K), the values of % saturation were corrected to that of 10 g animals, using the mean $(b-1)$ value of all groups. A weight of 10 g was used rather than unit weight

TABLE 1

Apparent water-permeability of Carcinus *as indicated by per cent D_2O-saturation in 15 min, with the hourly water exchange fractions* (K) *and probability* (t-*test*) *that differences are significant. Values adjusted to body weight of 10 g*

‰ SW	*n*	Mean % sat.	Standard deviation	Standard error	*K*	*P*
94	23	44.64	±5.48	1.14	2.36	
						> 0.05
75	11	49.54	±5.62	1.69	2.73	
						0.01
50	12	40.44	±4.29	1.24	2.07	
						< 0.025
25–35	22	35.62	±5.32	1.13	1.76	> 0.01

because 10 g was near the mean weight of the animals used, and so reduced possible errors of extrapolation. The hourly water exchange fraction (K) is given by the equation, $K = (2.3/t)\ \mathrm{Log}_{10}\ (100/100 - \%\,\mathrm{Sat.})$, in which K = per cent of body water exchanged per hour (assuming all water is exchangeable), t = time of exposure to D_2O in hours, % Sat. = % concentration of D_2O in water of blood at 15 min, referred to external D_2O concentration as 100%. The data from 25 and 35‰ SW, being indistinguishable, were pooled and are shown in Figures 1 and 2 as from 30‰ SW.

RESULTS

The influx of D_2O into *Carcinus* is relatively greater in smaller individuals. Curves showing the % saturation of D_2O in the blood as a function of weight after a 15-minute exposure to media containing D_2O are drawn in Figure 1. The slopes of the curves vary from −0.0757 to −0.1316 averaging −0.1088.

The adjustment of individual % saturation values to a body weight of 10 g provides the data shown in Table I and plotted in Figure 2. The specimens of *Carcinus* used in these experiments showed the greatest uptake of D_2O in 75‰ SW, with a slight reduction ($P > 0.05$) in 94‰ SW, and a significant reduction of

uptake in 50% and 30% SW (P *ca.* 0.01). Calculation of the hourly water exchange fractions (K) at each salinity yields values of 2.73 in 75% SW and a low value of 1.76 in 30% SW. Like *Rhithropanopeus*, *Carcinus* reduces its water exchange or its apparent permeability to water at low salinities.

The chloride concentrations of the blood of *Carcinus* in the different salinities of these experiments are shown in Figure 3 and in Table III, line 2. Chloride is strongly hyper-regulated at lower salinities, is isotonic with that of the medium at about 80% SW, and is hypo-regulated in SW. By computations which are explained in the Discussion, the net diffusional (osmotic) influx of water into *Carcinus* at each salinity was calculated (this involved certain assumptions as to

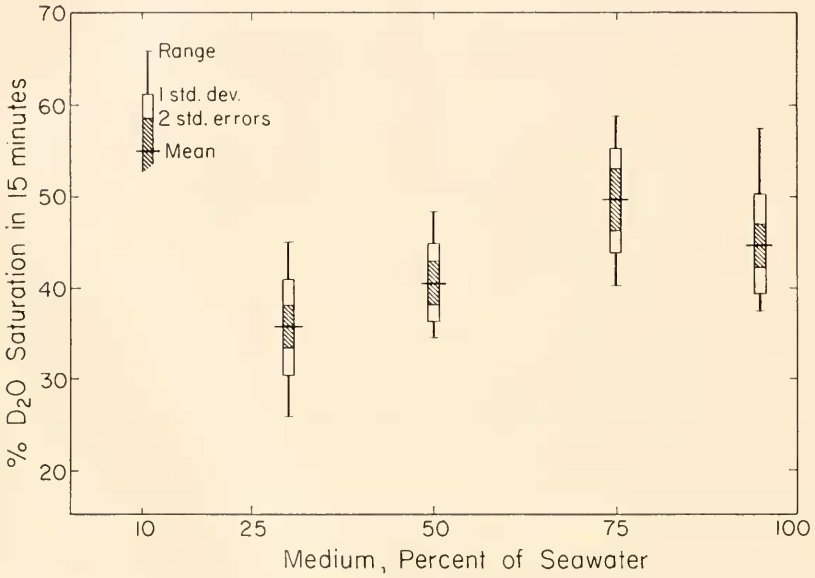

FIGURE 2. Per cent D_2O-saturation attained by *Carcinus* in 15 min as a function of salinity, corrected to a body weight of 10 g (see text). The values in 94% SW are not significantly lower than those in 75% SW ($P > 0.05$), although higher ($P < 0.05$) than those in 50% SW.

the osmotic pressure of the blood) and the results are shown in Table III, line 11. The calculated net water influxes in 50% and 75% SW correspond almost exactly to the volumes of urine produced by *Carcinus* at these salinities, as measured by Shaw (1961) and Binns (1969), shown on lines 13 and 14 of Table III. The calculated net influxes at any salinity are very much higher than those reported by Rudy (1967), but it will be shown in the Discussion that this discrepancy can be largely although not wholly eliminated if the sizes of animals and the temperatures are allowed for. The method of calculating net water influx provides for no net influx of water into *Carcinus* in SW, since the animal is presumed to be isosmotic with its medium; hence the present calculated net influxes and those of Rudy fail to account for the production of urine by *Carcinus* in SW, as observed by Shaw and by Binns. Likewise, neither the present results nor those of Rudy after

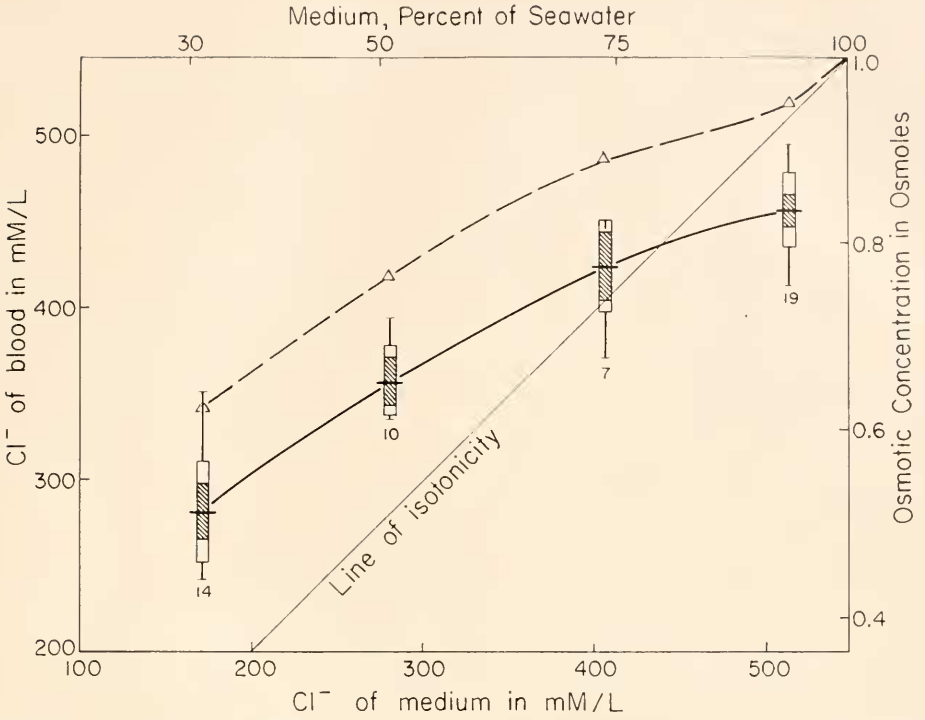

FIGURE 3. Chloride concentration of blood of *Carcinus* (left ordinate) as a function of chloride concentration of medium (bottom, Cl in m*M*/l; top, % SW). The upper broken curve shows assumed osmotic concentration of blood (right ordinate), as used for calculations in text and Table III. Figures below blocks are numbers of animals sampled.

adjustment for size and temperature (Table III, lines 11 and 12) account fully for the large production of urine in 40% SW measured by Shaw and by Binns (Table III, lines 13 and 14).

DISCUSSION

In discussing the reduced water exchange exhibited by *Carcinus* and *Rhithropanopeus* (Smith, 1967) at low salinities, it should be made clear that an effect and not a mechanism is being described. It is possible that the observed effect is the result of a reduction in the permeability of the integument to water, but in this discussion it is appropriate to use the term "apparent permeability" because no estimate of permeable surface area can be given, and because the effect upon D_2O exchange rate could as well result from a reduction in circulation of blood or irrigation of the gills as from a reduction in cuticular or epidermal water-permeability.

The small reduction in D_2O exchange rate seen in 94% SW is significant only between the 5% and 10% levels of probability, but such an effect is physiologically reasonable and may be expected in certain crustaceans, namely those which show hypo-osmotic regulation at higher salinities. *Carcinus* has not been shown to be a

hypo-osmotic regulator, but it may be noted (Fig. 3) that the crabs used in the present study hypo-regulated chloride in SW, and were isotonic in respect to chloride in about 80% SW. Although a measure of osmotic concentration would be more revealing than chloride concentration, this finding, together with the possibly lower apparent permeability in 94% SW, suggests that water-permeability lowering might be looked for under both hyper- and hypo-saline conditions in crabs which are normally exposed to such extremes in nature. Hypo-osmotic regulation has been reported in a number of brackish-water crabs, including some with terrestrial tendencies (Jones, 1941; Gross, 1964), although *Carcinus* is reported to be iso-osmotic or slightly hyperosmotic in SW (Robertson, 1960, and others). Rudy (1967) found that *Carcinus* in his study showed chloride-isotonicity in SW. A clue to the discrepancy between my chloride values and those of Rudy may exist in the finding by Ballard and Abbott (1969) that *Callinectes,* a fully aquatic crab of the same family as *Carcinus* (Portunidae), is hyper-osmotic in SW at 23–24° C, but hypo-osmotic in SW at 28–30° C. Rudy's specimens of *Carcinus* were adapted and tested at 10° C, mine were adapted at *ca.* 15° C and tested at 18° C, hence it is possible that his animals were hyper-osmotic, mine iso-osmotic, in SW. In future studies of *Carcinus* the relationship between adaptational temperature and osmotic concentration of the blood should be critically examined.

In order to compare the present results on *Carcinus* with those of Smith (1967) on the very small *Rhithropanopeus* and with those of Rudy (1967) on larger specimens of *Carcinus,* the earlier data have been recalculated for a body weight of 10 g. In recalculating Rudy's results, the mean $(b-1)$ value of -0.1088 obtained in the present study has been used. The K values so determined are shown in Table II. *Carcinus* in the present study shows higher water exchange fractions (K) than does *Rhithropanopeus*; the K's for the latter (based on D_2O uptake) averaging 39% those of *Carcinus* as indicated by the same isotope. This lower water exchange fraction is consistent with the conclusion that the more euryhaline *Rhithropanopeus* has a lower permeability to water than does *Carcinus.*

When Rudy's data for *Carcinus* (based on T_2O influx at 10° C) are corrected for a weight of 10 g, the K values (Table II) are so far below those of the present study that they have simply been doubled (assuming a Q_{10} of 2) to give values that can be compared with mine obtained at 18–19° C. The Q_{10} of 2 is close to the mean value of 1.90 found by Evans (1969) for water influx in fish. But even with this temperature correction, Rudy's K values for *Carcinus* average only 80% those of the present study.

Are the present data on *Carcinus* (based on D_2O) any more or less reliable than the data of Rudy based on T_2O? Correction of the latter values by reasonable assumptions about weight and temperature leaves a 20% difference in the hourly water exchange fractions, with the K values based on D_2O higher than those based on T_2O. It may be significant that K values for *Palaemonetes varians,* obtained by Rudy (1967) using T_2O, average only 50% of the values obtained on this same species by Parry (1955) using D_2O (Table II). Sufficient data are not available to permit corrections for weight and temperature but, as Rudy remarks, such corrections would probably not account for the whole of the large discrepancy. Obviously needed are water exchange values based on simultaneous T_2O and D_2O uptake measurements on the same species in order to decide whether the K values

TABLE II

Comparisons of hourly water exchange fractions (K) *based on D_2O and T_2O methods:* Rhithropanopeus harrisi, *for weights of 1 g and 10 g, recalculated from Smith (1967);* Carcinus maenas *for weight of 10 g;* Palaemonetes varians *of unspecified weights. See text for rationale of weight and temperature corrections*

Animal	*Rhithropanopeus harrisi* (1 g)		*Rhithropanopeus harrisi* (10 g)		*Carcinus maenas* (10 g)			*Palaemonetes varians* (unspec. weight)	
Isotope	T_2O	D_2O	T_2O	D_2O	T_2O		D_2O	T_2O	D_2O
Reference	Smith unpub.	Smith 1967	Smith unpub.	Smith 1967	Recalculated from Rudy, 1967		This paper	Rudy 1967	Parry 1955
Temp. °C	18–20°	18–20°	18–20°	18–20°	10°	20°	18–19°	10°	?
120% SW								0.64	1.61
94–100% SW		1.55		0.99	0.98	1.96	2.36		
70–75% SW	1.19	1.46	0.71	0.94	0.97	1.94	2.73	0.64	0.95
40–50% SW		1.27		0.85	0.90	1.80	2.07		
25–35% SW		1.05		0.70			1.76		
10% SW	0.75	1.00	0.47	0.67				0.55	
5% SW		0.98		0.65					1.31
1% SW		0.89		0.60					
$\frac{K\ (T_2O)}{K\ (D_2O)}$	0.78		0.73		—	0.80		0.50	

yielded by T_2O and D_2O represent an isotope effect or result from individual differences in method. Lacking such a simultaneous experiment with the two isotopes of water, the nearest that can be cited is an unpublished experiment (1968) in which I repeated the 1967 experiments with *Rhithropanopeus*, using T_2O. Without going into detail except that counts were on equal volumes of blood and medium added directly to the scintillation fluid, the results confirmed the change of apparent permeability with salinity in *Rhithropanopeus*, and yielded *K* values averaging 73–78% of the *K* values obtained with D_2O (Table II). This general agreement in the ratio of water exchange values independently arrived at with T_2O and D_2O in the separate experiments on *Rhithropanopeus, Carcinus*, and *Palaemonetes* suggests possibly the presence of an isotope effect causing a faster uptake of D_2O than of T_2O. However, the magnitude of this effect cannot be precisely stated because the recalculation of Rudy's data on *Carcinus* has involved a chain of assumptions.

Despite possible isotope effects, there is no reason to suppose that *relative* water-permeabilities are not fairly represented in comparative studies using either D_2O or T_2O. Rudy's values for the relative water-permeability of the series of crustaceans he studied using T_2O seem valid, and the relative differences in the apparent water-permeability of *Carcinus* as a function of salinity on the basis of D_2O in the present study likewise appear valid. It is suggested, however, that the water influx indicated by D_2O may be somewhat closer to the actual water influx of the animal. In order to test the reasonableness of the water exchange (K) values obtained on *Carcinus*, calculations from these values of net diffusional (osmotic) water influx have been made for comparison with reported values of urine production.

Rudy (1967) calculated the water fluxes of *Carcinus* on the basis of T_2O-exchange fractions (K), and on the assumptions that the osmolarity of SW is 1.0, that the water content of *Carcinus* is 70%, and that the osmolarity of its blood can be represented as % SW based on chloride concentration (in effect, as twice the blood chloride molarity). In the following recalculations I have, in general, followed Rudy's method to facilitate comparison, but have approached the problem of blood osmolarity with somewhat different assumptions. This has been necessary because *Carcinus* in my experiments showed hypotonicity of chloride in SW (Fig. 3) and approximate isotonicity of chloride in 80% SW, whereas Rudy found the chloride concentration of the blood of *Carcinus* in SW to be equal to that of the medium.

Since SW in my experiments had an average chloride concentration of 549 mM/l, its chlorosity is close to 19.1 ‰ (Barnes, 1954) and its freezing point is −1.88° C (Pantin, 1946), corresponding to an osmolarity of 1.01 osmoles. Rudy's assumption of a 1.0 osmolar concentration of SW is thus reasonable, but to apply the same method to blood is not advisable. Nagel (1934) reported that the chloride concentration of the blood of *Carcinus* (as NaCl) accounted for only 88% of the observed freezing-point depression. Lacking a direct measure of osmotic concentration in the animals used in the present study, I have recalculated the osmotic concentration of the blood of *Carcinus* in 94% SW as equivalent to $460 \times (100/88) = 523$ mM NaCl, an increase of 63 mM/l over the chloride concentration of 460 mM/l. The chloride concentration of the blood at lower salinities has then been arbitrarily raised by the same absolute amount, and the osmolarity expressed as % SW (Fig. 3 and Table III, lines 3 and 4). The osmotic concentration of the blood of *Carcinus* in 100% SW has been assumed to be equal to that of SW. By the use of such osmotic concentration values, net water influxes have been calculated by the following steps (data in Tables II and III): *e.g.*, in 30% SW, the mole fraction of water in medium = 55.56/(55.56 + 0.30) = 0.9946 (line 5); the mole fraction of water in blood = 55.56/(55.56 + 0.63) = 0.9888 (line 6); the mole fraction difference = 0.0058 (line 7). This difference accounts for the *net* water influx, which is equal to 0.0058/0.9946 = 0.58% of the total daily influx (line 10). Assuming a 70% by weight water content in *Carcinus* and that all water is exchangeable, the total daily water influx = $K \times 70\% \times 24\text{h} = 2957\%$ of body weight in water exchanged per day (line 9). *Net* influx is $0.0058 \times 2957 = 17.2\%$ of body weight per day (line 11). The results of this and similar calculations are shown in Table III, together with the urine volumes of *Carcinus* as

TABLE III

Calculation of daily net water influxes in Carcinus *at different salinities (line 11) for comparison with urine volume estimates of Shaw, 1961 (line 13) and Binns, 1969 (line 14). The net water influx values in line 12 are recalculated from data of Rudy (1967), adjusted for a body weight of 10 g and 20° C. See text for method of computation*

1. Medium, % seawater	30	50	75	94	100
2. Chloride concentration of blood, m*M*/l	282	359	427	460	—
3. Estimated osmotic concentration of blood as m*M* NaCl/l	345	422	490	523	—
4. Adjusted osmotic concentration of blood as % SW	63	77	89	95.3	assume 100
5. Mole fraction water of medium	0.9946	0.9911	0.9867	0.9834	0.9823
6. Mole fraction water of blood	0.9888	0.9863	0.9842	0.9831	0.9823
7. Mole fraction difference	0.0058	0.0048	0.0025	0.0003	0.0000
8. Hourly water exchange fraction (*K*)	1.76	2.07	2.73	2.36	assume 2.36
9. Daily water influx ($K \times 70 \times 24$) as % body weight per day	2957	3478	4586	3965	3965
10. Daily *net* water influx as % of total influx	0.58	0.48	0.25	0.03	nil
11. Daily net influx as % body weight (present data), tested at 18° C	17.2	16.7	11.5	1.19	nil
12. Daily net influx as % body weight (Rudy, 1967), recalculated for 20° C	16.8 (40% SW)	—	9.9	—	nil
13. Daily urine volume as % body weight (Shaw, 1961), 16° C	31.3 (40% SW)	16.5	11.1	—	3.6
14. Daily urine volume as % body weight (Binns, 1969), 9° C	21.1 (40% SW)	16.9	10.8	—	4.4

measured by Shaw (1961) at *ca.* 16° C (line 13) and by Binns (1969) at 9° C (line 14), and net water influxes recalculated from Rudy's data (1967) adjusted to a weight of 10 g and 20° C (line 12).

It does not appear feasible to make a meaningful estimate of the urine volume of *Carcinus* as a function of temperature. If the osmotic concentration of the blood

of *Carcinus* behaves as does that of *Callinectes* (Ballard and Abbott, 1969), being inversely related to temperature, then a lowering of water exchange (K) at low temperatures might be to an unknown degree counterbalanced by an increased osmotic gradient favoring a higher net water influx and greater urine volume. Obviously needed are determinations of the osmotic concentrations of the blood at the temperature of the experiment rather than or in addition to chloride determinations, and direct determinations of urine output as a function of temperature.

The net water influxes and urine volumes shown in Table III support the hypothesis that diffusional (osmotic) entry of water accounts for the urine production of *Carcinus* at intermediate salinities (50–70% SW). But if there is no osmotic gradient, *Carcinus* in SW must utilize some form of isotonic water transport. Such transport, in the absence of an osmotic gradient and by the expenditure of metabolic energy, is well known in vertebrates, and several possible mechanisms have been postulated (Diamond, 1965). Any mechanism of isotonic water transport operative in SW might also operate at lower salinities, and so would increase the net water influx above that calculated on the basis of diffusion. Some such mechanism appears necessary in 30–40% SW, where the calculated diffusional net water influx is well below the reported urine production (Table III). Alternatively, one might consider a system such as that suggested by Ussing (1954), in which inner diffusional areas are in series with outer pore-like spaces such that, once a diffusional net influx is established, a bulk flow of water is set up in the "pores" of sufficient velocity to counteract or reduce diffusion in the opposite, outward, direction. Such a system would have the properties of a rectifier or one-way valve, admitting water but restricting the outward diffusion of water below what would be expected on the basis of the water concentration in the blood. The water thus prevented from diffusing out would be available for disposal in the urine, over and above the net diffusional influx calculated from the mole fraction difference between water concentrations in blood and medium. The diffusional influx would be as expected; what would be reduced is the diffusional efflux.

It is evident that the water economy of *Carcinus* is still incompletely understood. Future work could profitably be directed to several problems. Is the apparent reduction of water-permeability with salinity the result of a reduction of circulation, either in the medium bathing gills or gut or in the circulation of the blood, or is it the result of an actual change of integumental permeability? The possibility that permeability reduction may accompany either hyper- or hypo-osmotic regulation seems physiologically adaptive and reasonable, but more critical examination is needed. This should be studied in some crab normally exposed to seasonal hypersaline conditions (Gross, 1961). The problems of correlating the water-permeability figures reported by different workers using T_2O and D_2O might be solved by simultaneous double-tracer studies of water influx in order to reduce individual operational variation and to evaluate possible isotope effects. In all such work the weights of the animals used must be taken into account and temperature controlled, since hourly water exchange fraction (K) varies with body weight as well as with salinity and temperature, and is thus no more a constant for a species than is respiratory rate.

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Summary

1. The apparent water-permeability of *Carcinus maenas*, as measured by D_2O influx, is 2–3 times higher than that of the more euryhaline crab *Rhithropanopeus*.

2. Like *Rhithropanopeus*, *Carcinus* shows a reduction of water-exchange rate at lower salinities. The highest hourly water-exchange fraction is in 75% SW ($K = 2.73$), the lowest in 30% SW ($K = 1.76$); values refer to a crab with wet weight of 10 g, at 18° C.

3. The calculated net diffusional (osmotic) water influx is adequate to account for the urine production of *Carcinus* in 50–70% SW, but does not account for urine production in SW, and only inadequately for the urine produced in 30–40% SW, and it seems necessary to postulate some isotonic transport of water.

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